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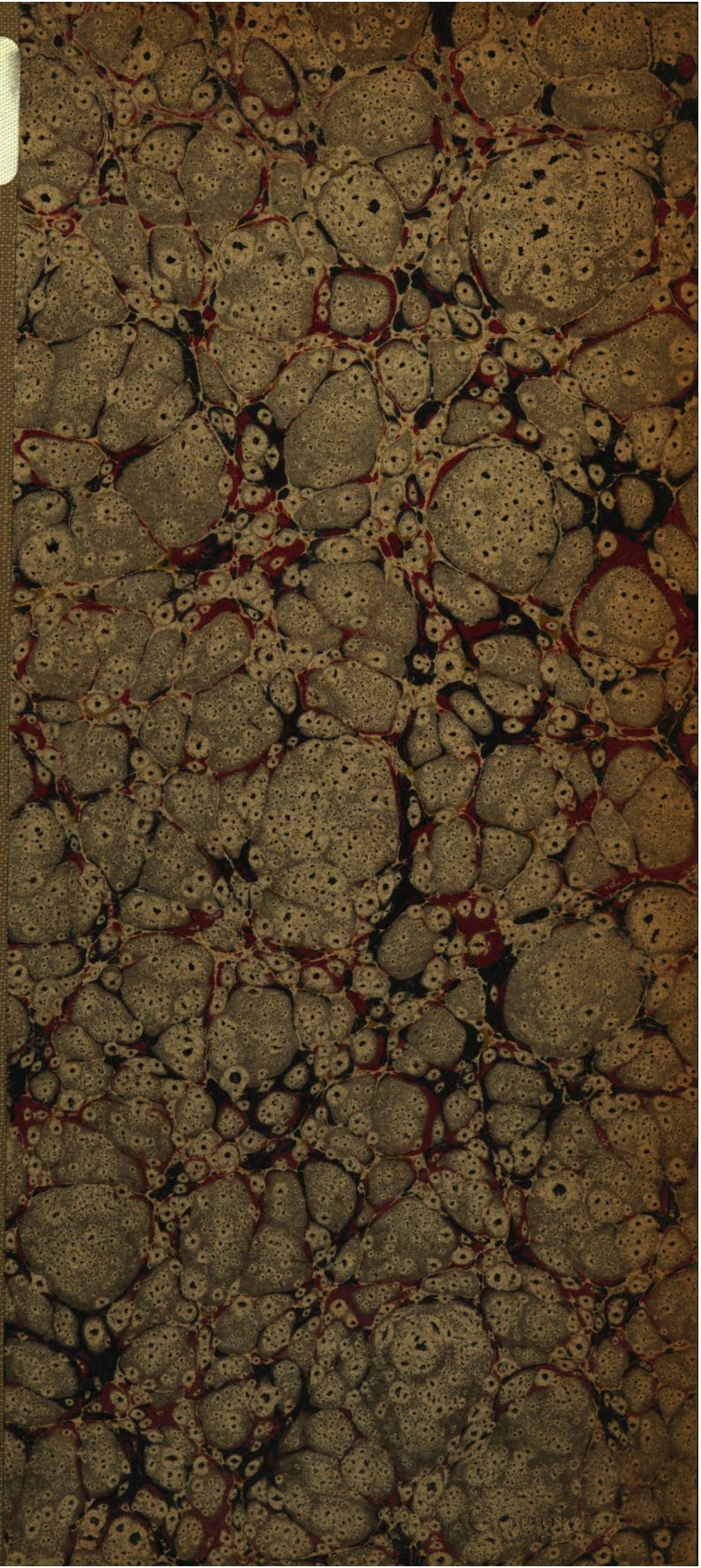
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(1886)

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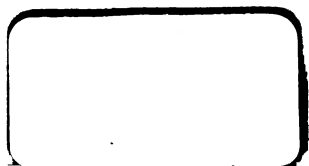
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ENTOMOLOGY.

THE ORGAN OF SMELL IN ARTHROPODS.¹—The question whether olfactory impressions as such are received by the Arthropoda,

¹ Abstract by A. S. Packard of a historical and critical study by Dr. K. Kræpelin. Separatdruck aus dem Osterprogramm der Realschule des Johanneums. Hamburg, 1883.

also whether there are specifically formed organs for the perception of this kind of sensation, has always been assumed in the affirmative sense. The naturalists of the previous century have recorded an abundance of observations, which have proved the highly-developed powers of smell at least in insects and Crustacea.¹

The existence of a definite sense of smell in the greater number of Arthropoda is, as Perris says, "a fact for a long time secured to science, for which there is need neither of arguments nor of proofs." Under these circumstances, it is clear that the question as to the seat of the sense of smell in the Arthropods has for a long time aroused the interest of naturalists. An extensive literature on this subject has grown up in the course of years, names of the first rank appearing in the history of these researches; though perhaps in no field of zoological knowledge has such an abundance of acute, difficult work had so small a following as in the examination of the organs of sense, and we are still this day, in spite of the great advance in the last ten years, far from a complete solution of the question.

Historical Sketch of our Knowledge of the Organs of Smell.—In the first half of the last century began the inquiries as to the seat of the sense of smell in the Arthropods. Thus Réaumur, in his *Mémoires* (I, p. 283; II, 224), expressed in different places the view that in the antennæ was situated a special organ which might be an organ of smell.

In a similar way Lesser,² Roesel,³ Lyonet,⁴ Bonnet⁵ and others expressed themselves. Before this Sulzer⁶ suggested that an "unknown sense" might exist in the antennæ. All these naturalists supposed that there was a common plan in the organization of all animals, and that they must agree with the structure of man. Hence some regarded the antennæ as two completely separate nasal halves, while others compared these appendages to the ears of mammals; others regarded the stigmata as organs of smell, or these were considered the natural passages for the olfactory currents. The oldest advocate of this view appears to have been Reimar⁷; following him, without knowing of the former's opinion, was Baster (1762). Finally, in the last decennial of the

¹ Scarcely less numerous are the observations and experiments which are recorded in literature as to the perception of sounds by Arthropods. I refer only to the Bala-ninus, by Bendorf; the caterpillar, by Bonnet; beetles and gnats, by Kirby; locusts, by Brunelli and Lehrman; the observations of Perris, Lespès, Landois, Rudow and others. Finally, Graber, in his latest work on "The Chordotonal Organs of Sense of Insects," p. 76, remarks: "For the first time exact proof has been afforded that insects in general become influenced by clear sound stimuli."

² Lesser: *Insecten theologie*, 1740, 262.

³ Roesel: *Insektenbelustigungen*, 1746, II, 51.

⁴ Lyonet: *Traite anatomique de la chenille*, 1762, 42, 96, 195.

⁵ Bonnet: *Œuvres complètes*, 1779-1783, II, 36.

⁶ Sulzer: *Geschichte der Insekten*, 1761.

⁷ Reimar^{us}: *Ueber die Triebe der Thiere*, 1760, 355.

preceding century, Duméril, in two special treatises as well as in his "Considérations générales," sought to prove this theory as to the seat of the organs of smell in the stigmata, while Schelver thought this view to be at least "not improbable."

Against both of these leading views as to the seat of the sense of smell were expressed, in the last century, different opinions. Thus Comparetti¹ thought that the sense of smell might be localized in very different points of the head, in the antennal club of Lamellicorns, in the sucking tube of Lepidoptera, in special frontal holes of flies and Orthoptera, etc., while Bonsdorf considered the palpi as organs of smell.

Thus were four different views, mixed together, given at the opening of this century; the Hamburg zoölogist, M. C. S. Lehrman, in three different treatises (2, 3, 4), brought together all the hitherto known observations and arguments, treated them critically, and completed them by his own extended studies. Lehrman adopted the opinions of Reimarus, Baster, Duméril and Schelver, that the stigmata presented the most convenient place for the site of the organs of smell; but he is the first who sought to afford a basis for these views by new experiments and also by anatomical data. Regarding the antennæ he was familiar with a number of anatomical details which in part had already been discovered before he wrote, viz, the entrance of a nerve from the brain into each antennæ,² the existence of muscles (Comparetti) and "vessels" (Bonsdorf) in them, etc. Cuvier followed throughout the lead of Lehrman, but Latreille³ returned to the view of the perception of smell by the antennæ, while Treviranus (7, 8), in different journals, considered the mouth of Arthropods as the probable site of the sense of smell, an opinion which, before his time, Huber,⁴ in his experiments on bees, had thought to be correct. In 1811 Rosenthal (5) published his discovery of an undoubted organ of smell at the base of the inner antennæ of crabs, and expressed his opinion that in the fly-like animals the sense of smell was probably localized in the folded frontal membrane above the base of the antennæ. This last conclusion seemed so logical to his contemporaries that even Burmeister, in his *Handbuch der Entomologie*, unhesitatingly accepted it. Less ready assent was given to Ramdohr's discovery, also in 1811, that the organ of smell could be found in the shape of a special vesicle in the head of bees, for the author himself afterwards acknowledged his discovery to be erroneous. A third publication of the same year by Marcel de Serres (26) returned again to the palpi, and asserted—at least in the Orthoptera—their functions to be olfactory, while Blainville,⁵ ten years later, again expressed anew the

¹ *Comparetti*: De aure interna comparata, Patavii, 1769.

² *Scarpa*: De auditu et olfactu, Ticini, 1789.

³ *Latreille*: Histoire Naturelle des Crustacés et des Insectes, 1806–1809, II, 50.

⁴ *Huber*: Nouvelles Observations sur les Abeilles, 1792, II, 475.

⁵ *Blainville*: Principes d'Anatomie Comparée, 1822, I, 339.

old opinion that the antennæ, or at least their terminations, were organs of smell. Up to that date there was an uncertainty as to the seat of the organs both of smell and hearing. Fabricius (57), indeed, had already, in 1783, thought he had found an organ of hearing at the base of the outer antenna; but this opinion was negatived by Rosenthal's discovery of an organ of smell [*sic*] in the inner antennæ of crabs; but as regards the insects, which have but a single pair of antennæ, the question stood at the old point, and it remained a matter of speculation whether this single pair of antennæ had the power of perceiving sounds or smell, or finally, both kinds of sense-impressions. In 1826 appeared J. Müller's valuable work, "*Vergleichende Physiologie des Gesichtsinnes*," in which this naturalist spoke of an already well-known organ in the thorax [abdomen] of crickets as an organ of hearing. Müller, however, was doubtful, from the fact that the nerve passing to this organ arose, not from the brain, but from the third thoracic ganglion; but, notwithstanding, he remarks: "Perhaps we have not found the organ of hearing in insects because we sought for it in the head." This discovery was afterwards considerably broadened and extended by Siebold's work,¹ for the views of these naturalists on the seat of both organs had a definite influence, especially in Germany. At present, indeed, Müller's hypothesis stood in complete contradiction, so that during the following decennial was presented anew the picture of opposing observations and opinions as to the nature of the organs of smell. While Robineau-Desvoidy, at the end of the twentieth year, and also later, in different writings (27, 34), strove energetically for the olfactory nature of the antennæ, Strauss-Dürkheim² held fast to the view that the tracheæ possessed the function under discussion. At the same period Kirby and Spence, in their valuable *Introduction to Entomology*, maintained that "two white cushions on the under side of the upper lip" in the mouth of biting insects formed a nose or "rhinarium" peculiar to insects. This opinion was afterwards adopted by Lacordaire (*Introduction à Entomologie*, II), and also by Oken in his *Lehrbuch der Naturphilosophie*, while Burmeister, rejecting all the views previously held, believed that insects might perhaps smell "with the inner upper surface of the skin." Müller's locust's ear he regarded as a vocal organ.

Besides these occasional expressions of opinion, the French literature of the thirtieth and fortieth years of this century recorded a long series of special works, with weighty experimental and physiological contents, on this subject. Thus Levebre, in 1838 (28), described the experiments which he made on bees, and

¹ v. Siebold: Ueber die Stimm- und Gehörorgane der Orthopteren, *Archiv für Naturgeschichte*, Jahrgang 10, I, 52-87, 1844.

² Strauss-Dürkheim: *Considérations générales sur l'Anatomie Comparée des animaux articulés*, etc. Paris, 1828, 422.

which seemed to assign the seat of the sense of smell to the antennæ. Dugès¹ reported similar researches on the Scolopendræ, and Pierret (32) thought that the great development of the antennæ in the male Bombycidæ might be similarly interpreted. Driesch (29) sought to give currency to the views of Bonsdorf, Lamarck and Marcel de Serres, that the sense of smell was localized in the palpi, though Duponchel (30, 31) went back to the old assertion of æroskepsis of Lehrman, *i. e.*, of the air-test through the antennæ, and Goureau (33) again referred the seat of the sense of smell to the mouth. In England, Newport (45) at this period put forth a work in which he considered the antennæ as organs of touch and hearing, and the palpi as organs of smell—a view which, as regards the antennæ, was opposed by Newman (43).

Thus the contention as to the use of the antennæ and the seat of the organs of smell and hearing fluctuated from one side to the other, and when in 1844 Küster (9), by reason of his experiments on numerous insects, again claimed that "the antennæ are the smelling organs of insects," he argued on a scientific basis; yet v. Siebold and Stannius (1848), in their valuable *Lehrbuch der vergleichenden Anatomie* (p. 581), remarked that "organs of smell have not yet with certainty been discovered in these animals."

These naturalists were more happy with the crabs, whose organs of smell, with Rosenthal, they localized in the vesicle at the base of the inner antennæ, though Farre (46) had regarded these cavities as possessing the function of hearing.

The following decennial was of marked importance in the judgment of many disputed questions. Almost contemporaneously with Siebold and Stannius' *Lehrbuch* appeared an opportune treatise by Erichson (10), in which this naturalist first brought forward certain anatomical data as to the structure of the antennæ of insects. In a great number of insects Erichson described on the upper surface of the antennæ peculiar minute pits, "pori," which, according to him, were covered by a thin membrane, and to which he ascribed the perception of smell. A still more thorough work on this subject was published in the following year by Burmeister (11), who recognized in the pits of Lamellipeds many small tubercles and hairs; and about the same time Slater (12), as also Pierret and Erichson before him had done, out of the differences of the antennal development in the males and females in flesh and plant-eating insects, brought together the proof of the olfactory function of the antennæ. But the most valuable work of this period is that of Perris (36), who, after a review of previous opinions, by exact observations and experiments, a model of their kind, sought to discover the seat of the sense of smell. He comes to the conclusion that the antennæ,

¹ *Dugès: Traité de Physiologie Comparée*, 1838, I, 160.

and perhaps also the palpi, may claim this sense, and finds full confirmation of Dufour's (37) views, and adopts as new the physiological possibility expressed by Hill¹ and Bonnet,² that the antennæ might be the seat of both senses—those of smell and hearing.

As for the Crustacea, it was through Huxley,³ and still more through Leuckart,⁴ that the evidence was afforded that Rosenthal's—also adopted as such by Blainville—olfactory organ at the base of the inner antennæ should be regarded as an apparatus of hearing. Huxley therefore thought, following Farre and Robineau-Desvoidy, that the seat of the sense of smell must lie in the organ discovered by Fabricius in the outer antenna, while Leydig,⁵ almost at the same time, considered certain pale, minute hairs on the terminal joint of the inner antennæ as specific sense-organs.

The beautiful works of Erichson, Burmeister and Perris could not remain long unnoticed. In 1857 Hicks (47, 48, 49) published complete researches on the peculiar nerve-endings which he had found in the antennæ, also in the halteres of flies and the wings of all the other groups of insects,⁶ and which he judged to be for the perception of smell. But Erichson's and Burmeister's "pori" were by Lespès, in 1858 (38), explained to be so many auditory vesicles with otoliths. This view was refuted by Claparède (39) and Claus (13), without their deciding on any definite sense.—*To be continued.*

¹ Hill: Hamburger Magazin, xvii, 391.

² Bonnet: Contemplation de la Nature, III C, 18.

³ Huxley: On the Auditory Organs in the Crustacea, Ann. and Mag. Nat. Hist. II Ser. Vol. vii, 1851.

⁴ Leuckart: Ueber die Gehörwerkzeuge der Krehse, Archiv für Naturgeschichte, 1853, I, 255, 304–306, 373–374.

⁵ Leydig: Ueber Artemia salina und Branchipus stagnalis, Zeits. f. w. Zoologie, III, 1851, 287.

⁶ Graber's sketch of our earlier knowledge of the "peg-bearing" organs (the chordotonal sense-organs of insects) pp. 509, 558, 586, are therefore to be corrected in the foregoing sense.

ENTOMOLOGY.

KRAEPELIN ON THE ORGANS OF SMELL IN ARTHROPODS.¹—To Leydig it was first given to make a decided step in advance. In different writings² had this naturalist busied himself with the integumental structures of Arthropods, and declared Erichson's view as to the olfactory nature of the antennal pits as the truest, before he, in his careful work on the olfactory and auditory organs of crabs and insects (14), gave excellent representations of the numerous anatomical details which he had selected from his extensive researches in all groups of Arthropods. Besides the pits which were found to exist in Crustacea, Scolopendræ, beetles, Hymenoptera, Diptera, Orthoptera, Neuroptera and Hemiptera, and which had only thus far been regarded as sense-organs, Leydig first calls attention to the widely-distributed pegs and teeth, also considering them as sense-organs. "Olfactory teeth," occurring as pale pegs, perforated at the end, on the surface of the antennæ of Crustacea,³ Myriopoda, Hymenoptera, Lepidoptera, Coleoptera, are easily distinguished, and besides the "olfactory pegs" of the palpi, may be claimed as organs of smell. The nerve-end apparatus first discovered by Hicks in the halteres and wings, Leydig thinks should be ranked as organs of hearing.

Regarding the Crustacea, Leydig, in his latest work,⁴ gave a lasting explanation of the nature of the pale peg or cylinder on the end of the antennæ which he found in new groups of this class, which was adopted by a large number of naturalists. Thus Claus,⁵ in his different essays, expressed the view that these Leydigian organs had the function "of making sensible slight changes in the chemico-physical condition of the water." Indeed, in his later essays⁶ he without hesitation calls the structures in question "olfactory teeth," while he at the same time offers a series of anatomical data on the finer structure of the same. Entirely

¹ Translated by A. S. Packard. Concluded from p. 894.

² *Leydig*: Zum feineren Bau der Arthropoden, Müller's Archiv, 1855, 376-480; Zur Anatomie der Insekten, Archiv für Anatomie, 1859, pp. 35-89 and 149-183; Lehrbuch der Histologie, 1857, 220.

³ These pegs, as occurring in Asellus and Daphnidæ, had already been well described, in 1860, in his monograph "Naturgeschichte der Daphiden," Tübingen, 1860, without, however, a discussion of the question whether they were olfactory organs.

⁴ *Leydig*: Ueber Amphipoden und Isopoden, Zeits. f. w. Zoologie, xxx, 1878, 225-274.

⁵ *Claus*: Ueber die Organization und Verwandtschaft der Copepoden, Würzburg, 1862, 19; Die freilebenden Copepoden, Leipzig, 1863, 55.

⁶ *Claus*: Entwicklung, Organization und Systemat. Stellung der Arguliden. Zeit. f. w. Zool., 1875. Zur Kenntniss der Organization und des feineren Baues der Daphniden, etc. Zeits. f. w. Zool., 1876. Zur Kenntniss des Baues, und der Organization der Polyphemiden. Denkschr. d. Wiener Akad. wiss. Math. Naturw. Classe, 1877, xxxvii, 245. Der Organismus der Phronimiden, Wien, 1879, 10.

in the same direction do Sars,¹ Weismann,² Rougemont,³ Gamroth,⁴ Hoek,⁵ Haller⁶ and others more or less decide upon the olfactory nature of the organ of Leydig.

Jourdain (40) does not accept this opinion, and Wrzësniewski⁷ adopted the views of Milne-Edward and La Valette. The "calceoli" of Amphipoda might be regarded as organs of smell.

There was still some opposition to Leydig's opinion that in the insects the sense of smell is localized in the antennæ (teeth and pits), and here the work of Hensen⁸ might be mentioned, which in 1860 had a decided influence upon the conclusion of some inquiries.

Thus Landois (15) denied that the antennæ had the sense of smell, and declared that the pits in the antennæ of the stag beetle were auditory organs. In like manner Paasch (16) rejected Leydig's conclusion, while he sought to again reinstate the old opinion of Rosenthal as to the olfactory nature of the frontal cavity of the Diptera. In spite of the exact observations and interesting anatomical discoveries of Forel⁹ in ants, made in 1874, there appeared the great work of Wolff on the olfactory organs of bees, in which this observer, with much skill and acuteness, sought to give a basis for the hypothesis of Kirby and Spence that the seat of the sense of smell lay in the soft palatine skin of the labrum within the mouth. Joseph (18), two years later, drew attention to the stigmata as olfactory organs, referring to the olfactory girdle, and Forel¹⁰ sought by an occasional criticism of Wolff's conclusions to prove experimentally the olfactory function of the antennæ; but Graber,¹¹ in his much-read book on insects, defended the Wolffian "nose" in the most determined way, and denied to the antennæ their so often vindicated faculty of smell. In 1879 Berté (52) thought he had observed in the antenna of the flea a distinct auditory organ, and Lubbock¹² considered the organs of

¹ Sars: *Historie naturelle des Crustacés d'eau douce de Norvège*, Christiania, 1867.

² Weismann: *Ueber den Bau und der Lebenserscheinungen der Leptodora hyalina*, Zeits. f. w. Zool., xxiv.

³ Rougemont: *Naturgeschichte des Gammarus puteanus*, München, 1875, 9.

⁴ Gamroth: *Beiträge zur Kenntniss der Naturgeschichte der Caprellen*, Zeits. f. w. Zool., xxxi, 1878.

⁵ Hoek: *Carcinologisches in Tydschr. d. Md. Dierk. Vereen. Deel*, iv, 102.

⁶ Haller: *Der Læmadipodes filiformes*, Zeits. f. w. Zool., xxxiii, 1880, 368.

⁷ Wrzësniewski: *Vorl. Mittheilung über einige Amphipoden*. Zool. Anzeiger, 466, 1879.

⁸ Hensen: *Das Gehörorgan der Decapoden*. Zeits. f. w. Zool. xiii, 1863. *Das Gehörorgan von Locusta*. Zeits. f. w. Zool. xvi, 1886.

⁹ Forel: *Les Fourmis de la Suisse*. Neue Denkschr. Allg. Schweiz. Gesellsch. f. d. ges. Naturw. xxvi, 1874. 118, 144.

¹⁰ Forel: *Der Giftapparat u. d. Anal-drüsen der Ameisen*. Zeits. f. w. Zool. xxx. Suppl. 60.

¹¹ Graber: *Die Insekten*, München, 1877.

¹² Lubbock: *On some points in the anatomy of ants*. Monthly Micr. Journ., 1887, 121-142.

Forel in the antennæ of ants as a "microscopic stethoscope." In 1879 Graber described a new otocyst-like sense-organ in the antennæ of flies (20) which was accompanied by a complete list of all the conceivable forms of auditory organs in Arthropods. In this work Graber described in *Musca* and other Diptera closed otocysts with otoliths and auditory hairs, as Lespè had previously done. But Paul Mayer, in two essays (21, 53) refuted this view in a criticism of the opinion of Berté, referring the "otocysts with otoliths" to the well-known antennal pits into which tracheæ might pass. Mayer did not decide on the function of the hairs which extend to the bottom of the pits; while in the most recent research, that of Hauser (22), the author again energetically contended for the olfactory function of the antennæ. Both through physiological experiments and detailed anatomical investigations Hauser sought to prove his hypothesis as Pierret, Erichson, Slater, and others had done before him, besides working from a Darwinian point of view. In a purely anatomical aspect, especially prominent are his discovery of the singularly formed nerve-rods in the pits and peg-like teeth of the Hymenoptera and their development, as well as the assertion that numerous hairs in the pits described by Leydig, Meyer, etc., should be considered as direct terminations of nervous fibers passing into the pits. In the pits he farther, with Erichson, notices a serous fluid, which may serve as a medium for the perception of smells. Among the latest articles on this subject are those of Künckel and Gazagnaire (41) which are entire anatomical, while the latest treatise of Graber on the organs of hearing in insects¹ opposes Hick's theory of the olfactory function of the nerve-end apparatus in the halteres, wings, etc., and argues for the auditory nature of these structures. Finally, experimental researches by Voges on the seat of the olfactory organs are only known to the writer by a notice in the "Täglichen Rundschau."² According to this observer the sense of smell is not localized, but spread over the whole body.

¹ *Graber*: Ueber die Chordotonalen Sinnesorgane der Insekten. Archiv. f. mikrosk. Anat. xx, 506-640. xxi, 65-145, 1881, 1882.

² *Tägliche Rundschau*. Zeitung für Nichtpolitiker, 1882, September (?).



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